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The evolution of eyes in the Bivalvia: New insights*

Brian Morton

Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K., prof_bmorton@hotmail.co.uk

Abstract: Two types of multi-cellular eyes have been identified in the Bivalvia. Paired cephalic eyes occurring internally above the anterior end of the ctenidia are seen only in representatives of the Arcoidea, Limopsoidea, Mytiloidea, Anomioidea, Ostreoidea, and Limoidea. These eyes, comprising a pit of photo-sensory cells and a simple lens, are thought to represent the earliest method of photoreception. Many shallow-water marine, estuarine, and freshwater bivalves also possess simple photoreceptive cells in the mantle that enable them to respond to shadows. In some other marine, shallow-water taxa, however, a second type of more complex photoreceptors has evolved. These comprise ectopic pallial eyes that can be divided into three broad categories, in terms of their locations on the (i) outer mantle fold in representatives of the Arcoidea, Limopsoidea, Pterioidea, and Anomioidea, (ii) middle fold in the Pectinoidea and Limoidea, and (iii) inner fold in the Cardioidea, Tridacnoidea, and Laternulidae (Anomalodesmata). Eyes do not occur in deep-sea bivalve taxa. Where ectopic pallial eyes occur, they measure amounts of light and integrate intensities from different directions, thereby supplying information to the individual possessing them about the distribution of light in its immediate environment. This does not mean, however, despite broad, phylogenetically related advances in pallial eye complexity, that any bivalve can perceive an image. A revised picture of the independent evolution of ectopic pallial eyes in the Bivalvia is provided. In bivalves, pallial fold duplication has resulted in improvements to the peripheral visual senses, albeit at different times in different phylogenies and on different components of the mantle margin. This has been achieved, it is herein argued, through: (i) selective gene-induced ectopism; (ii) pigment cup evagination in Category 1 eyes; (iii) invagination in Categories 2 and 3; and (iv) natural selection. The invaginated distal retina in representatives of the Pectinidae and Laternulidae provides the potential for image formation and the detection of movement. In the absence of optic lobes capable of synthesizing such information, however, these complex eyes must await matching cerebral sophistication.

Key words: cephalic and pallial eyes, evagination, invagination, duplication, mantle folds

A wide range of internal proprioreceptors and external sense organs has evolved in the Bivalvia. The former includes muscle proprioreceptors to moderate muscle tonus and, uniquely, in the watering pot shells (Clavagellidae and Penicillidae), a pair of pericardial proprioreceptors to monitor body tonus (Morton 2007). The latter sense organs include paired statocysts (for orientation), osphradia for the reception of chemical spawning cues and synchronization of gamete emission (Beninger *et al.* 1995), abdominal (Haszprunar 1985) and pallial sense organs, as in *Aulacomya atra* (Molina, 1782) (Zaixso 2003), both for the mechanoreception of water currents, and light-sensitive cephalic and pallial eyes (Morton 2001). These are structures that can measure amounts of light and integrate intensities from different directions, thereby supplying information to the individual possessing them about the distribution of light in its immediate environment (Land and Nilsson 2002). As will be argued, however, the presence of such light-sensitive structures does not necessarily mean, despite phylogenetically related advances in pallial eye complexity, that any bivalve eye, in the absence of significant integrative optic lobes in the cerebral ganglia, can perceive an image of its immediate environment.

When present, cephalic eyes are located internally on the left and right sides of the body at the base of the anteriormost filaments of the inner demibranchs of the ctenidia but have been seen and described only for representatives of the Arcoidea, Limopsoidea, Mytiloidea, Anomioidea, Ostreoidea, and Limoidea (Morton 2001). The eyes, each comprising a pit of photo-sensory cells and a simple lens, are thought to represent the earliest method of photoreception in the Bivalvia, but their functional efficiency must be constrained by the fact that, in life, light would be received by them after transmission through the thickest part of the shell in epibenthic taxa and from the posterior in the case of most infaunal species. More recent bivalves do not possess such eyes (Morton 2001).

Kennedy (1960) described the simplest pallial photoreceptor known for the Bivalvia. He demonstrated that the pallial nerves of *Spisula solidissima* (Dillwyn, 1817) each con-

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tain a single light-sensitive afferent nerve fiber. This responds directly to illumination and mediates the shadow response (or reflex) of siphonal retraction. Because the shadow reflex is so widespread in freshwater and coastal bivalves, it can be assumed that most of them possess such sensory fibers. Even, for example, in the absence of any obvious photoreceptors, *Donax vittatus* (da Costa, 1778) responds to changes in incident light intensity by adjusting its position in the sediment (Ansell *et al.* 1998). Conversely, the subterranean freshwater dreissenid *Congeria kusceri* Bole, 1962 does not possess such a reflex (pers. obs.) and no multi-cellular pallial eyes have evolved in freshwater, brackish-water, or deep-water bivalves. Only intertidal and shallow continental shelf species possess them.

A few other coastal bivalves have, however, evolved more sophisticated pallial photoreceptors. In a few taxa, such structures have resulted in the evolution of pallial eyes of extraordinary (for such sedentary creatures) structural complexity. Morton (2001) reviewed such eyes in the Bivalvia and showed that pallial photoreceptors could be divided into three categories (typically associated with an increasing degree of morphological specialization) based upon their locations on the (i) outer, (ii) middle, or (iii) inner mantle folds. As will be also discussed, some progress has been made in understanding how the development of eyes is controlled genetically, most recently reviewed by Gehring (2001), but the objectives of this paper are to understand (i) how the pattern of increasing pallial eye sophistication has come about and (ii) how, for each category of eye (Morton 2001), its various components have been assembled.

CEPHALIC EYES

It is believed that molluscan cephalic eyes can be derived from structures similar to those that occur in planarians, themselves representative of those that would have been found in the ancestor(s) of all metazoans. Gehring (2001), quoting Hesse (1897), believes that the eyes of *Planaria torva* are the most likely candidates for and examples of such an ancestor. Each *P. torva* eye comprises three photoreceptor cells surrounding a single pigment cell (Fig. 1). The cephalic eyes of bivalves are only somewhat more complex and the larvae of oysters, for example, *Crassostrea virginica* (Gmelin, 1791) and *Crassostrea gigas* (Thünberg, 1793), develop a pair of light-sensitive eyespots (Nelson 1926) that gradually start to degenerate soon after metamorphosis (Baker and Mann 1994). In species of *Chlamys* Röding, 1798, *Pecten* Müller, 1776, and *Ostrea* Linnaeus, 1758, such eyespots consist of a cup of pigmented cells surrounding an amorphous (unstructured) lens (Cole 1938, Cragg and Crisp 1991, Hodgson and Burke 1998). Cole (1938) has described the cephalic eye in

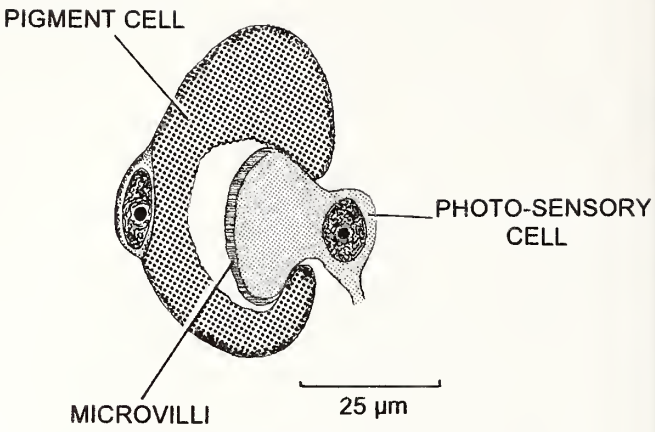

Figure 1. A section through the eye of the flatworm *Planaria torva*. Redrawn after Hesse (1897).

the pre-settlement veliger of *Ostrea edulis* Linnaeus, 1758 (Fig. 2) and notes that each one is situated on the body wall just dorsal to where the gill rudiments attach and, oppositely, to the mantle.

Cephalic eye structure in the Bivalvia appears to be highly uniform (Morton 2001). This suggests that such eyes must have a common ancestry and may once have been much more widespread in the class but have subsequently either been lost or never developed in the majority of taxa. Those of *Aulacomya atra* (Mytilidae) can serve as an example of cephalic eye structure and have been described by Zaixso

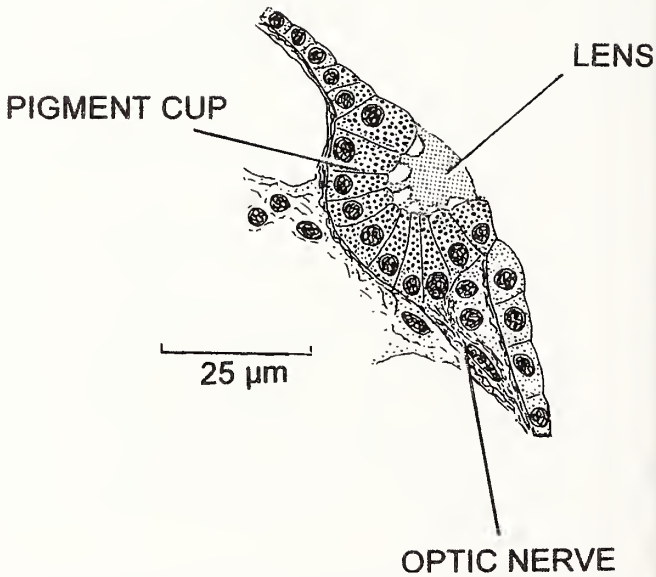

Figure 2. A section through the cephalic eye of the pre-settlement veliger of *Ostrea edulis*. Redrawn after Cole (1938).

(2003). One such eye is illustrated in section (Fig. 3). It comprises a cup of pigmented and photo-sensory cells enclosing a simple, amorphous, lens. Nerve fibers arise basally from the photo-sensory cells to connect up with the cerebropleural ganglia. Such an eye structure is similar to that of *Philobrya munita* (Finlay, 1930) and of *Pteria brevialata* (Dunker, 1872) (Morton 1978, 1995).

PALLIAL EYES

Category 1: Pterioidea, Arcoidea, Limopsoidea, and Anomioidea

Pterioidea: Pteria brevialata

Morton (1995) has described the mantle margin and pallial eyes of *Pteria brevialata* (Pteriidae). Although the mantle margin appears to comprise the usual bivalve three folds (Yonge 1982), it does not. Instead, the outer mantle fold is sub-divided into two sub-folds comprising (i) a specialized inner photo-sensory component on which are located the pallial eyes (Category 1: Morton 2001) and (ii) external to this an outer component that secretes the shell. Both sub-folds are, therefore, overlain by the shell and two-layered periostracum when the mantle is retracted and the pallial eyes thus monitor light even through the periostracum when the mantle margin is extended. The pallial eyes of *P. brevialata* are among the simplest multi-cellular optical structures yet described for the Bivalvia and comprise simple photo-sensory cells located on the outer epithelium of the inner component of the outer mantle fold and are backed on the opposite, inner, epithelium by a patch of pigmented cells (Fig. 4). Nerve fibers arise from the bases of the photo-sensory cells and pass towards the pallial nerve.

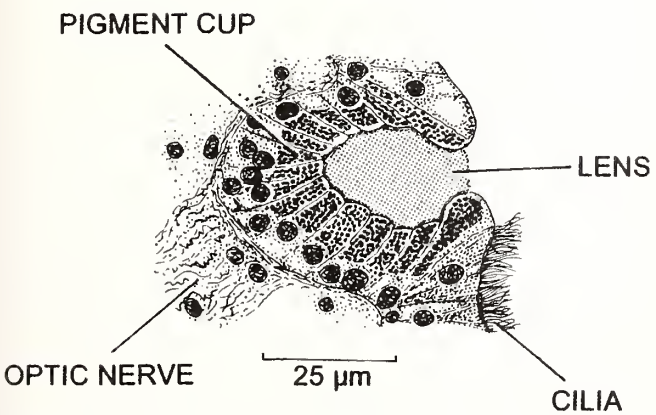

Figure 3. A section through a cephalic eye of *Aulacomya atra*. Redrawn after Zaixso (2003).

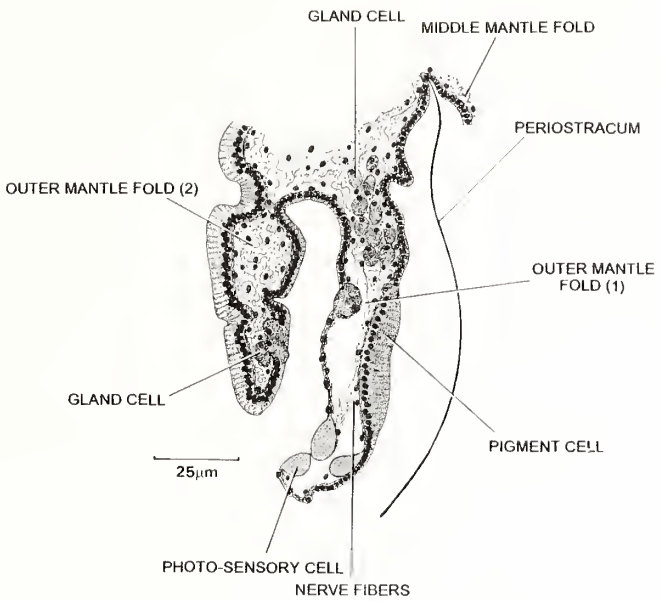

Figure 4. A section through the simplest known pallial eye of the outer mantle fold of *Pteria brevialata* (Category 1). Redrawn after Morton (1995).

Arcoidea and Limopsoidea

Representatives of the Arcoidea (and Limopsoidea) possess two types of pallial eyes, namely multi-faceted compound eyes and simple pigment cups. Both types may occur in the same species but both develop on the inner sub-fold of the outer mantle fold and are, as a consequence, covered by the periostracum even when the mantle margins are expanded, as in *Pteria brevialata* described above.

Arca noae

The mantle margin of *Arca noae* Linnaeus, 1758 is illustrated in section (Figs. 5 and 6B) (after Morton and Peharda 2008). The pallial eyes of *A. noae* are of the compound ommatidial type first described by Waller (1980, 1981), their fine structure subsequently elucidated by Nilsson (1994). Each, of many hundreds, compound eye of *A. noae* is located on the inner sub-fold of the outer mantle fold and comprises photosensitive cells surrounded by and intermixed with pigment cells. In *A. noae*, the plump stalk and mantle beneath each eye are also pigmented, perhaps enhancing their photo-sensory efficiency.

Barbatia virescens

The second eye type seen in representatives of the Arcidae (and Limopsoidea) is a pigment cup or invaginate eye. One of the pallial eyes of *Barbatia virescens* (Reeve, 1844) (Fig. 6A), also located on the inner sub-fold of the outer mantle fold (Morton 1987), comprises a simple cup of intermixed photo-sensory cells and pigment cells. The cup

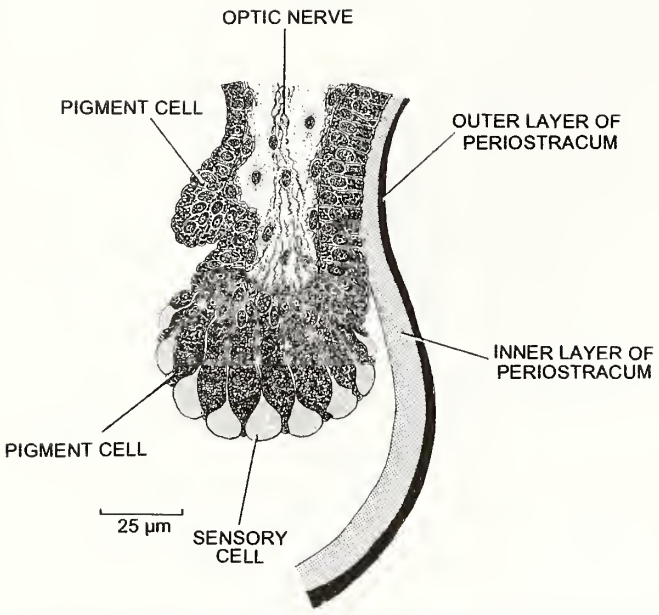

Figure 5. A section through the pallial eye of the outer mantle fold of *Arca noae* (Category 1). Redrawn after Morton and Peharda (2008).

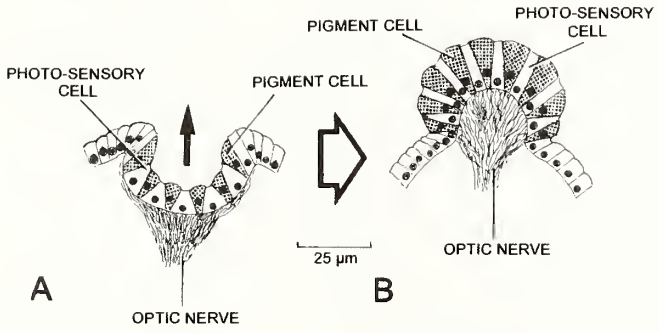

Figure 6. Sections through the simple cup-like pallial eye of A, *Barbatia virescens* (Redrawn after Morton 1987) and B, the ommatidial pallial eye typical of representatives of the Arcoidea (both Category 1).

encloses an amorphous lens and the eye is thus similar to the bivalve cephalic eye.

As will be discussed, the compound ommatidial eye (Fig. 6B) might have evolved by evagination from the simpler invaginate eye (Fig. 6A). For example, the limopsid *Philobrya munita* (Finlay, 1930) has a pallial eye that is possibly intermediate between the inverted cup and compound ommatidial eyes (Morton 1978, fig. 4).

Anomioidea: Enigmonia aenigmatica

The pallial eyes of *Enigmonia aenigmatica* (Holten, 1803) (Anomiidae) are located, uniquely, on the general mantle beneath the shell (Morton 1976, fig. 2) and, thus, also the periostracum and have been described by Morton (2001, figs. 8 and 9). Each adult individual possesses ~22 cups of pigmented retinal cells that have invaginated from the inner epithelium of the general mantle surface. Above each cup is a more structured, cellular lens that is formed on the outer surface of the general mantle. There is also a ciliated accessory sense organ. It is unknown how this optical structure has been assembled from either (i) an invaginated cephalic eye pigment cup that has moved from its usual position or (ii) has migrated inwards from the mantle margin. The occurrence with each eye of an accessory ciliated sense organ is, however, unusual in that, as will be seen, such a structure is typical only of Category 3 eyes (those that occur on the inner mantle fold). Bearing in mind that *E. aenigmatica* lies on its right shell valve, it seems possible that the eyes have, in evolutionary terms, migrated inwards from the left mantle lobe to lie under the left shell valve. From which marginal fold, however, is unknown. The fact that the eyes perceive light through the shell, however, places them in Category 1 but they do constitute a unique photosensory structure in the Bivalvia.

Category 2: Limidae and Pectinidae

Limidae: Ctenoides floridanus

The pallial eyes of *Ctenoides floridanus* (Olsson and Harbison, 1953) are located on the middle mantle fold and have been described by Morton (2000a). One is illustrated in section (Fig. 7A). Each eye comprises a cup of photo-sensory cells surrounded laterally by pigment cells. Each sensory cell of *Lima scabra* (Born, 1778) has been shown by Bell and Mpitsos (1968) to possess bundles of cilia and basal neural processes. A large optical nerve arises from the base of the cup and there is a cellular lens. Interestingly, however, the

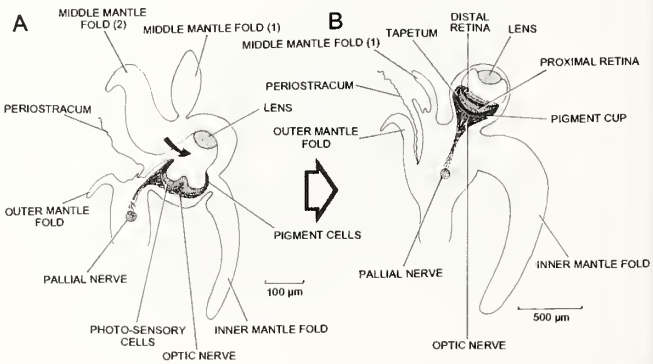

Figure 7. Simplified sections through the pallial eyes (Category 2) of A, *Ctenoides floridanus* and B, *Pecten pusio.* Redrawn after Morton (2001) and Patten (1886), respectively.

eye is not closed to the sea, but is open, and an amorphous plug of tissue occupies the space between retina and lens.

The importance of this invaginated eye is that it illustrates, as will be discussed, the manner in which bivalve ectopic pallial eyes have changed their locations in the Pteriomorphia from a specialized sub-fold of the outer mantle fold (and thus beneath the shell and periostracum) to the middle fold (and thus beyond the shell and periostracum).

Pectinidae: Pecten pusio

The eye of *Pecten pusio* (Linnaeus, 1758) (Fig. 7B) has been described by Patten (1886), and Dakin (1910, 1928) and Morton (1980, 1993, 1996, 2000b) have described the eyes of other pectinids, including species of *Spondylus* (Linnaeus, 1758), *Annusium* Röding, 1798, *Leptopecten* Verrill, 1897, *Minnivola* Iredale, 1939, and *Placopecten* Verrill, 1897. The eyes are located on the middle mantle fold with more on the mantle margin of the upper right valve than the lower left [see, for example, the description of *Annusium pleuronectes* (Linnaeus, 1758) by Morton (1980)].

The pectinid eye is the most well-known bivalve optical structure and has best been described for *Pecten maximus* (Linnaeus, 1758) in a series of papers by M. F. Land (see Morton 2001 for a review). This species and *Pecten pusio* uses a lens to focus light onto a parabolic mirror of pigmented cells, called the argentea, and reflecting this back onto the more distal of two, ciliary-based, retinal layers (Land 1965) where it is capable of defining an image. The proximal retina, on the other hand, detects changes in light intensity (Land 1966). Each retina possesses cilia with a 9 + 0 structure but the proximal one will be responsible for stimulating the typical escape response of free-living species of the Pectinidae, for example, the accomplished swimmer *Annusium pleuronectes* (Morton 1980).

Category 3: Myidae, Cardiidae, Tridacnidae, and Laternulidae

Myidae: Mya arenaria

Light (1930) demonstrated for *Mya arenaria* Linnaeus, 1758 that photosensitive tissue is located in the inner surface of the siphons, mostly at their tips, that is, the fused inner mantle folds. He further identified using silver nitrate staining and described light sensitive cells each containing an optic organelle composed of a large hyaline structure—the lens—surrounded by a network of nerve fibers that he called the retinella. Two of these cells are illustrated (Fig. 8).

Cardiidae and Tridacnidae: Cerastoderma edule *and* Tridacna maxima

The pallial eyes of representatives of the Cardiidae have been described by numerous authors, but the eyes of *Cerastoderma edule* (Linnaeus, 1758) are the most well-known

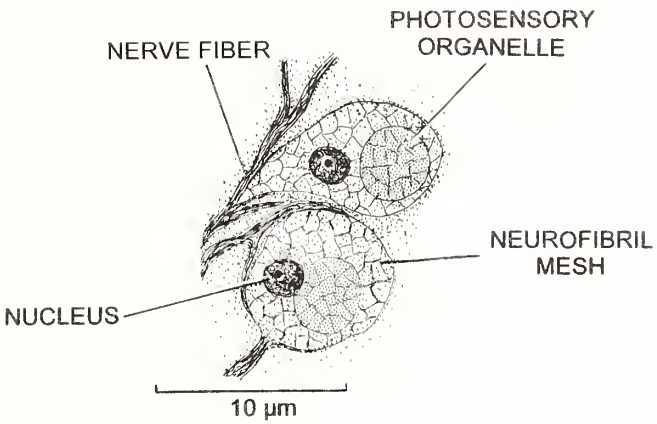

Figure 8. *Mya arenaria.* A section through two siphonal photoreceptors. Redrawn after Light (1930).

(Barber and Land 1967, Barber and Wright 1968). In an adult individual, ~60 of them occur on the inner folds of both mantle lobes each atop a siphonal tentacle. Each eye comprises a cup of pigmented cells enclosing 12-20 receptor cells. Each photo-sensory receptor cell has about 100 cilia, each with a 9 + 0 filament content (Barber and Land 1967) and with the optical nerve arising internally and departing the eye at the apical junction of the cup with the lens. Joining the optic nerve laterally is a nerve from a ciliated sense organ of unknown function. It is probably, however, a mechanoreceptor. Weber (1909) and Braun (1954, fig. 5) showed that the accessory sense organ of each pallial eye of *Cardium oblongum* Gmelin, 1791 actually comprises two clusters of cilia (Fig. 9). This is also true for the pallial eye of *C. edule* (Fig. 10A).

Representatives of the Tridacnidae also possess pallial eyes that are located as in the Cardiidae on the, albeit greatly expanded, inner mantle folds. An adult *Tridacna maxima* (Röding, 1798) will have thousands of eyespots but they have the same basic structure as those described (above) for representatives of the Cardiidae. As well as fulfilling a visual function, however, tridacnid eyes may focus light on masses of zooxanthellae residing around them in the mantle hemocoel, prompting Yonge (1936) to refer to them as hyaline organs (although still derived from true eyes). The light-receiving properties of the array of tridacnid eyes has been demonstrated by Stasek (1965) who showed that the shadow reflex results in a giant clam squirting a jet of 'aimed' water at any fish (or human) moving above it. The zooxanthellae might also, however, function as an accessory light reflecting pigment cup, enhancing the efficiency of the clearly photosensory eye apparatus and thereby confirming the truly symbiotic relationship that exists between the bivalve and its entrained phytoplankters.

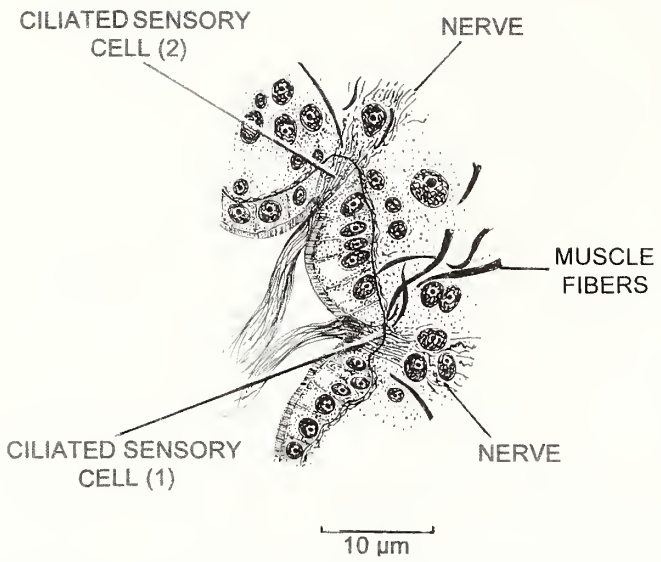

Figure 9. A section through the accessory, ciliated, sense organ of the pallial eye (Category 3) of *Cardium oblongum* Gmelin, 1791. Redrawn after Braun (1954).

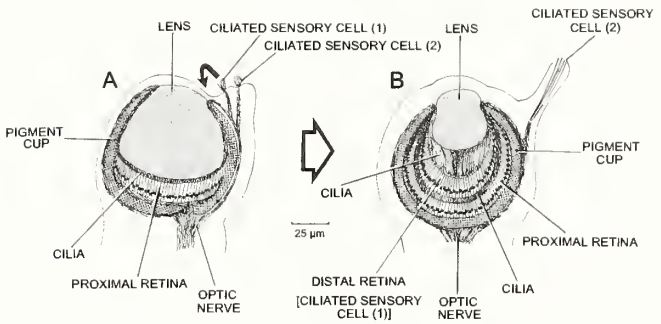

Figure 10. Simplified sections through the pallial eyes (Category 3) of *Cerastoderma edule* (after a number of authors) and *Laternula truncata*. Redrawn after Adal and Morton (1973).

Laternulidae: Laternula truncata

The Anomalodesmata comprises the most family-rich subclass of the Bivalvia and yet only representatives of the Laternulidae, for example *Laternula truncata* (Lamarck, 1818), have been shown to possess pallial eyes (Adal and Morton 1973) (Fig. 10B). As in *Cerastoderma edule*, each of the nine eyes sits atop a siphonal tentacle and is hence located on the inner mantle fold. As in representatives of the Pectinidae, for example *Pecten maximus* (Dakin 1910), there is a cup of pigment cells forming a parabolic mirror, or argentea, which encloses a double-layered, proximal and distal retina. The lens focuses light onto the argentea, which reflects it back onto the distal retina. In such a way, it is possible, as in representatives of the Pectinidae, to form an image. Morton (1973) showed, however, that the extremely sedentary infaunal *L. truncata*, which is capable of only slow burrowing, possesses only a shadow reflex that results in pallial tentacles attempting to flick sand grains over the exposed siphons. Presumably, if the situation is similar to that seen in representatives of the Pectinidae, the proximal retina is responsible for detecting changes in light intensities and thus stimulating the shadow reflex. The cells of each retina possess cilia that, again as in representatives of the Pectinidae, have a 9 + 0 structure (Adal and Morton 1973).

As in *Cerastoderma edule*, each pallial eye of *Laternula truncata* has an accessory sense organ except that in this species the groups of ~28 cilia with a 9 × 0 + 2 structure are long (50 µm) and contained within an invagination of a specialized tentacle (Adal and Morton 1973). Projecting from a pore at the apex of the tentacle, each cilium may make contact with the microvilli of the surrounding epithelium (as the tentacle moves) and is, hence, probably a mechano-receptor. The eyes of *L. truncata* represent a remarkable example of convergent evolution with those of representatives of the Pectinidae.

DISCUSSION

Gaten (1998) suggested that superimposition eyes, which re-direct light from many facets onto the target rhabdomeres, have evolved only once in the crustacean Decapoda, probably in the Devonian (345-395 mya). Morton (2001) similarly argued that in the Bivalvia, cup-like, cephalic eyes have probably also only evolved once but have been either retained by or developed in representatives of only a few (generally older) phylogenies (see above). Morton (2001) also showed, however, that, conversely, ectopic pallial eyes have evolved a number of times in various lineages of the Bivalvia and, typically, in different ways, notably with regard to their positions on the various folds of the mantle margin.

The sizes (diameters) of various bivalve pallial eyes are illustrated (Fig. 11) in relation to their category. What is obvious is that there is no clear relationship between eye category and size. That is, Category 1 eyes are all <~800 µm in diameter whereas Category 2 eyes all range in diameter between 100 µm and <1,000 µm. Category 3 eyes, however, are also only ~100 µm in diameter. Size does not seem to be an indicator of structural and, hence, optical complexity even though the pallial eyes of *Pecten maximus* (a large scallop) are among the largest and most sophisticated bivalve optical structures. Moreover, the pallial eyes of *Laternula truncata* are only 100 µm in diameter but are as morphologically complex as those of *P. maximus* (Adal and Morton 1980).

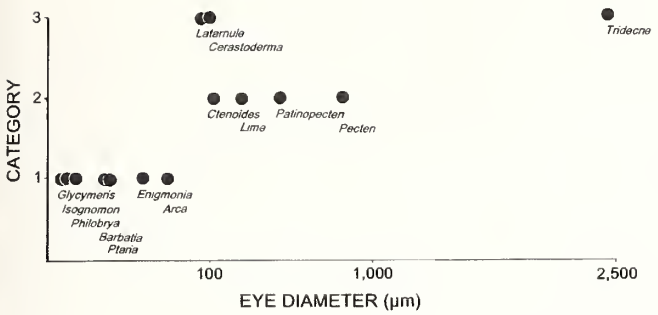

Figure 11. The pallial eye diameters of bivalves which are known to possess them and which have been divided into the three structural categories of Morton (2001). Note: x-axis scale is not uniform.

Furthermore, the eyes of representatives of the Tridacnidae (Fig. 11) are ~2.5 mm in diameter and hence about 25 times the size of those of their nearest relatives, the cardiid cockles. Although giant clams are the largest extant bivalves, their pallial eyes also have the same basic structure as representatives of the Cardiidae. It is, therefore, possible that tridacnid eyes are larger because, as well as fulfilling a visual function, they focus light on masses of zooxanthellae residing around them in the mantle hemocoel (Fankboner 1981, Wilkens 1986). The zooxanthellae might also, however, function as an accessory light-reflecting pigment cup. Excluding, therefore, as a special case, the hyaline organs/eyes of the Tridacnidae, it seems (Fig. 11) that all bivalve ectopic pallial eyes are of about the same size, probably in relation to the size of the individuals that possess them. Thompson (1942: 34-35) noted for a number of vertebrates that:

> *"A big dog's eye is hardly bigger than a little dog's; a squirrel's is much bigger, proportionately, than an elephant's; a robin's is but little less than a pigeon's or a crow's."*

Hence, as with Thompson's vertebrate examples, size alone is not an indication in the Bivalvia of either structural complexity or visual acuity. Nevertheless, the fact that some bivalves, for example representatives of the Arcoidea, Pectinidae, and Tridacnidae, possess so many pallial eyes suggests that they are highly important in another way. First, however, what controls pallial eye development?

The *Six1/2/so* and *Six3/6/7/9/optix* groups of genes are implicated in eye and sensory structure development. In *Drosophila*, *so* is associated with the eye marginal disc and Bolwig's organ, and the expression of *so* in the un-patterned epithelium is required for eye morphogenesis and development of the visual system (Cheyette *et al.* 1994). A mutation in the *so* homeobox disrupts the larval visual system of *Drosophila* and abolishes the larva's response to light (Hassan *et al.* 2000). The expression of *so* is regulated by *eyes absent* (*eya*) (Bonini *et al.* 1997) and the expression of both is required to induce ectopic eyes (Halder *et al.* 1998). However, Gehring and Ikeo (1999) considered *Pax6* and its homologs to be the control gene for eye development in metazoans although it is now known that a number of others (including *eya*), for example, *dachshund* (Shen and Mardon 1997) and *sine oculis* (Pignoni *et al.* 1997) are also able to induce ectopic eye expression in *Drosophila*. Serb (2008, fig. 1) provides a model of the network of genes that regulates eye formation in *Drosophila*.

In the case of the Bivalvia, however, the recovery of *so* sequences from *Nutricola tantilla* (Gould, 1853) and *Crassostrea gigas* by Bebenek *et al.* (2004) suggests that the ability to develop ectopic eyes is present in both taxa but neither has produced them, possibly because either *eya* or the other genes identified above are not present. Such a generalization might apply to the vast majority of bivalves (Fig. 12). However, Light (1930) appears to be the only person who has, once determining that *Mya arenaria* does have a shadow reflex, demonstrated, using silver nitrate staining, the presence and described the structure of intra-cellular light sensitive bodies mostly in the tips of the siphons. Since it is known that most shallow-water marine, estuarine, and freshwater bivalves do possess a shadow reflex, perhaps it would be beneficial if they too could be examined in more detail prior to arguing that *eya* and/or the other genes now associated with ectopic eye development (in *Drosophila*) are not present.

As described by Nilsson (1994), for representatives of the Arcidae, and reviewed by Morton (2001), the pallial eyes of those bivalves that possess them, regardless of their structural complexity, are analogous to photoreceptive burglar alarms that are placed on the outsides of (human) buildings. That is, although no image is discerned, only simple spatial movement, the efficiency of this optical sensory system has been refined in each of the three categories of eyes. How?

In the Arcoida, pallial eyes are restricted to species that inhabit shallow waters so that the deep-water *Bathyarca pectunculoides* (Scacchi, 1833) does not possess them (Morton 1982). The pallial eyes of *Barbatia virescens* and *Anadara notabilis* (Röding, 1798) are simple ciliated pits (Morton 1987, Nilsson 1994) whereas the compound ommatidial eyes of *Arca noae* conform in structure to those of other species of *Arca* (Waller 1980, 1981) and *Barbatia cancellaria* (Lamarck, 1819) (Nilsson 1994). Since the pallial eyes of representatives of the Arcoida (Category 1) comprise pigment cups which lack a well-defined lens and the cavity is filled with rhabdomeric microvilli arising from the receptor cells (Nilsson 1994), there are no cilia so that there is no base structure present for the evolution of a ciliary-based retina. Notwithstanding, an arcid compound ommatidial eye can be derived by evagination of a pigment cup (as illustrated in

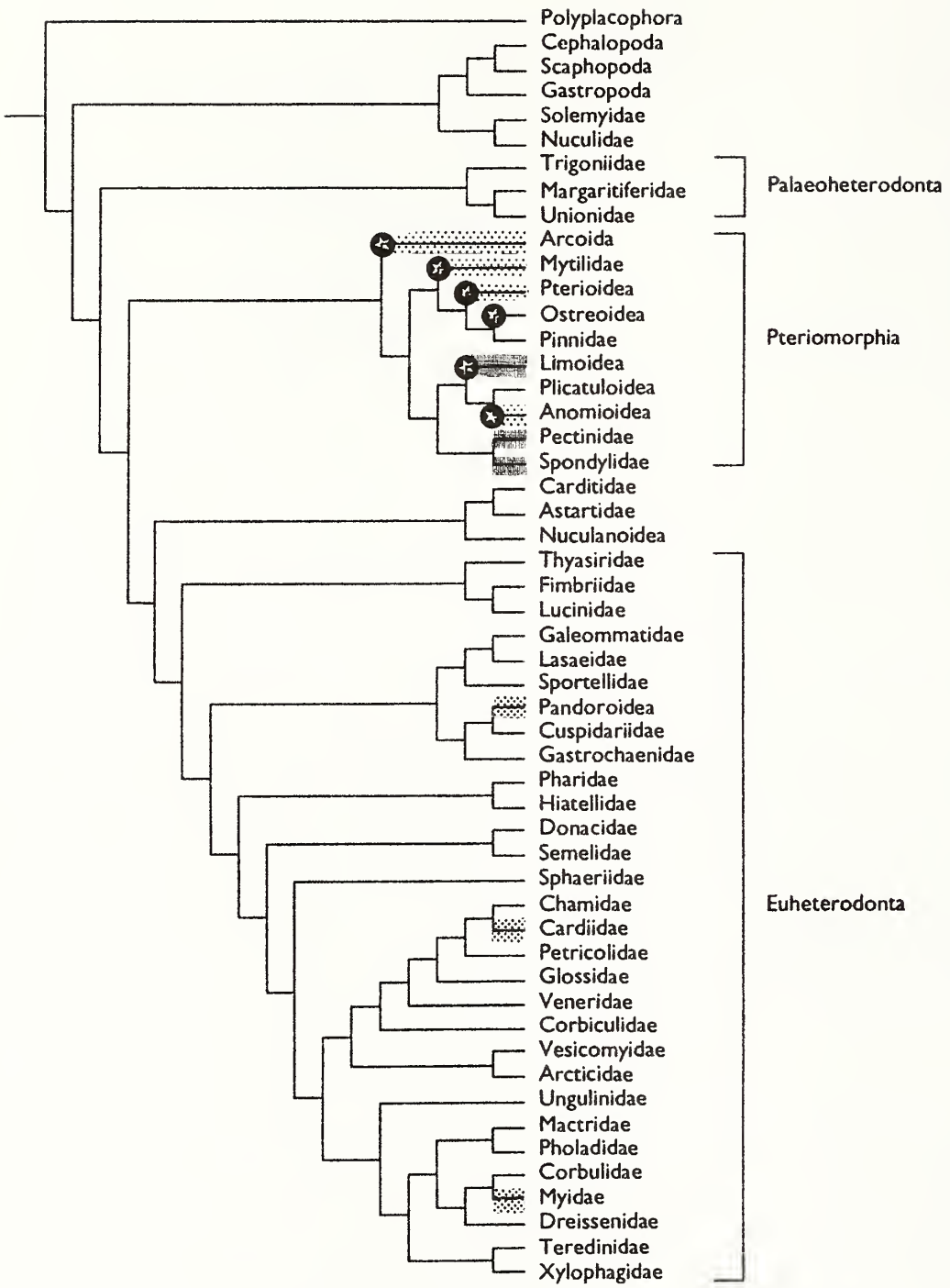

Figure 12. A phylogenetic tree of the Bivalvia based on Giribet and Distel (2004, fig. 3.6), showing the occurrence of cephalic eyes (stars) and ectopic pallial eyes belonging to Categories 1 (Arcoida, Mytilidae, Pteriodea, Anomioidea), 2 (Limoidea, Pectinidae, Spondylidae) and 3 (Pandoroidea, Cardiidae, Myidae).

Fig. 6) to create a structure that (i) has a greater breadth of view and which could (ii) but only in theory, produce a 'summed' image (Dawkins 1997). The limopsid *Philobrya munita* has a pallial eye that seems to be intermediate between the inverted cup and compound ommatidial eyes in that like the latter it is everted although pigment and photosensory cells are not inter-mixed (Morton 1978).

As Morton (2001) pointed out, however, no bivalve has any kind of brain that could ever recreate within it an image, regardless of the sensory sophistication of the eye that receives the enhanced differences in light associated with such improvements. The paired optic lobes of the cerebral ganglia of *Pecten maximus* are relatively 'large' for a bivalve (see Dakin 1909, plate 6, fig. 28) but nowhere near as large as

those of cephalopods, for example, *Octopus vulgaris* Cuvier, 1797 (see Wells 1968, fig. 9.7; Hanlon and Messenger 1996, fig. 2.8) and which possess some 65 million nerve cells (Young 1971) involved not only in visual analysis but also act as visual memory stores.

Moreover, the fact that some bivalves, notably representatives of the Arcoidea and Pectinidae, possess so many pallial eyes along the mantle margin suggests that the eyes are highly important. In what way? In the case of the Arcidae, the presence of many compound eyes may allow for the detection of movement, as each is stimulated in succession by a moving object (Nilsson 1994). The same probably applies to the parallel circlets of eyes along the left and right mantle margins of scallops.

However, because Category 1 eyes develop on the outer mantle fold under the shell and periostracum, what changes in light they detect must be of poor visual quality. They, thus, perceive only a passing shadow. A human eye with a lens cataract might provide an analogy. This is not so, however, in those bivalves that developed pallial eyes on either their middle (Category 2) or inner (Category 3) mantle folds since they develop beyond the shell and periostracum. The increased visual acuity associated with such 'external' locations has been enhanced further by increases in structural complexity. How might this have been achieved?

In the Limidae and Cardiidae, there are ciliated pallial tentacles or accessory ciliated sense organs, in the former and latter, respectively, located upon specialized sub-folds of the middle or inner mantle fold, again respectively. Representatives of those two only distantly related bivalve families with the most sophisticated retina-based eyes, that is, the Laternulidae and Pectinidae both possess a ciliary-based proximal retina (Barber and Land 1967, Bell and Mpitsos 1968). It seems possible, however, that invagination of either an adjacent ciliated sensory tentacle or accessory organ, respectively, and incorporation of such a structure into these eyes might explain how the ciliary-based distal retina has been developed in both of them (as illustrated in Figs. 7 and 10, respectively). This would further explain how the double retina eyes of representatives of both families have evolved. They are, hence, also, an example of convergent evolution.

It seems possible, therefore, that the duplication of structures, in these cases either sensory tentacles or accessory organs, opens up the potential not only for new structures to evolve but also to alter and enhance functions. Hence, the original proximal retina was and still is responsible for detecting changes in light intensity and thus stimulating the shadow reflex. However, the distal retina, derived from an invaginated ciliated accessory structure, provides the **potential** for image formation and the detection of movement in representatives of the Pectinidae and Laternulidae. In the absence of optic lobes capable of synthesizing such information, however, these complex eyes must await matching cerebral sophistication.

The Arthropoda provides a well-known example of how the duplication of appendages has facilitated not just ambulatory but also mandibular diversification resulting in the extraordinary adaptive radiation of the phylum's numerous representatives and, hence, also of their eyes (Oakley 2003). In the Bivalvia, pallial fold duplication has resulted in improvements to the total array of peripheral pallial senses, most notably, however, the visual one. Improvements to the pallial visual senses have, however, occurred at different times in different phylogenies and on different components of the mantle margin. This has been achieved through (i) selective gene-induced ectopism; (ii) pigment-cup evagination in Category 1 eyes; (iii) invagination of accessory structures in some eye Categories 2 and 3 to form a distal retina in representatives of the Pectinidae and Laternulidae; and (iv) natural selection.

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